Stronger saccadic suppression of displacement and blanking effect in children

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Humans do not notice small displacements to objects that occur during saccades, termed saccadic suppression of displacement (SSD), and this effect is reduced when a blank is introduced between the pre- and postsaccadic stimulus (Bridgeman, Hendry, & Stark, 1975; Deubel, Schneider, & Bridgeman, 1996). While these effects have been studied extensively in adults, it is unclear how these phenomena are characterized in children. A potentially related mechanism, saccadic suppression of contrast sensitivity—a prerequisite to achieve a stable percept—is stronger for children (Bruno, Brambati, Perani, & Morrone, 2006). However, the evidence for how transsaccadic stimulus displacements may be suppressed or integrated is mixed. While they can integrate basic visual feature information from an early age, they cannot integrate multisensory information (Gori, Viva, Sandini, & Burr, 2008; Nardini, Jones, Bedford, & Braddick, 2008), suggesting a failure in the ability to integrate more complex sensory information. We tested children 7 to 12 years old and adults 19 to 23 years old on their ability to perceive intrasaccadic stimulus displacements, with and without a postsaccadic blank. Results showed that children had stronger SSD than adults and a larger blanking effect. Children also had larger undershoots and more variability in their initial saccade endpoints, indicating greater intrinsic uncertainty, and they were faster in executing corrective saccades to account for these errors. Together, these results suggest that children may have a greater internal expectation or prediction of saccade error than adults; thus, the stronger SSD in children may be due to higher intrinsic uncertainty in target localization or saccade execution.

Introduction

Humans can execute multiple saccadic eye movements per second. With every saccade, the presaccadic stimulus features and location must be reconciled with their postsaccadic counterpart in order to maintain a stable percept of the world. The visual system may achieve this transsaccadic perceptual stability by integrating pre- and postsaccadic feature information (Demeyer, Graef, Wagemans, & Verfaillie, 2010a; Ganmor, Landy, & Simoncelli, 2015; Wijdenes, Marshall, & Bays, 2015; Wolf & Schütz, 2015; Stewart, Valsecchi & Schütz, in press) or location information (Cicchini, Binda, Burr, & Morrone, 2013; Prime, Niemeier, & Crawford, 2005), or by suppressing small displacements that occur during the saccade (Bridgeman, Hendry, & Stark, 1975). However, it is unknown when such mechanisms develop. While many visual processes such as integration and segmentation of basic visual features develop in the first few years of life (for review, see Braddick & Atkinson, 2011), other integrative processes such as optimal multisensory integration are still developing up until 8 to 10 years of age (Gori, Viva, Sandini, & Burr, 2008; Jovanovic & Drewing, 2014; Nardini, Jones, Bedford, & Braddick, 2008), and performance on more cognitively demanding saccade tasks such as antisaccades continues to develop until the age of 15 (Munoz, Broughton, Goldring, & Armstrong, 1998). In this study, we focus on the development of one process that contributes to transsaccadic perceptual stability—saccadic suppression of displacement (SSD)—and compare SSD and the blanking effect between children 7 to 12 years old and adults 19 to 25 years old. Measuring SSD in children gives us an

insight into when transsaccadic integrative processes may develop; measuring the blanking effect allows us to test whether the same information may also be segregated when correspondence between pre- and postsaccadic stimuli is broken. We additionally relate perceptual measures to saccade error metrics to explain how greater saccade variability may result in greater SSD.

Saccadic suppression of displacement and the blanking effect

SSD refers to the inability of observers to detect small stimulus displacements that occur during a saccade (Bridgeman et al., 1975). SSD is strongest when the stimulus displacements occur in an elliptical area along the axis of saccade direction (Wexler & Collins, 2014), and scales with saccade amplitude, such that larger displacements are undetected for larger saccade amplitudes (Bridgeman et al., 1975; Li & Matin, 1990; Li & Matin, 1997).

SSD is thought to arise from several aspects of visuomotor and perceptual processing. Contrast sensitivity during a saccade is strongly reduced, due to several factors, such as retinal image blur caused by high eye velocity (Burr & Ross, 1982; Castet, Jeanjean, & Masson, 2002; Castet & Masson, 2000; Ilg & Hoffmann, 1993); masking by the clear and strong input before and after the saccade (Campbell & Wurtz, 1978; Duyck, Collins, & Wexler, 2016), and an active reduction of sensitivity (Braun, Schütz, & Gegenfurtner, 2017; Burr, Holt, Johnstone, & Ross, 1982; Burr, Morrone, & Ross, 1994; Diamond, Ross, & Morrone, 2000). This phenomenon is called saccadic suppression of contrast sensitivity (SSCS). When a stimulus changes its position during fixation, a highly informative motion transient can be obtained (Tynan & Sekuler, 1982); however, if the displacement happens during a saccade, this transient is suppressed due to SSCS. The visual system must presumably then compare the observed presaccadic target position to the observed postsaccadic target position (evaluation on the underlying process can be found in the paragraphs below). The localisation ability of the visual system, however, is imperfect and diminishes with increasing eccentricity (Anderson & Yamagishi, 2000; Hess & Hayes, 1994; Levi & Tripathy, 1996; Michel & Geisler, 2011; Westheimer, 1982; White, Levi, & Aitsebaomo, 1992). The visual system could also use position information that comes from the execution of the eye movement itself, but this is itself noisy (Abrams, Meyer, & Kornblum, 1989; Frost & Pöppel, 1976; van Beers, 2007; van Opstal & Gisbergen, 1989; Vitu, Casteau, Adeli, Zelinsky, & Castet, 2017). Given these limitations, it does not seem surprising that the visual system has difficulties correctly perceiving intra-saccadic displacements. In addition, sudden

position changes of objects are statistically unlikely, and the visual system is believed to have a prior expectation that results in a bias for perceiving the environment as stable (MacKay, 1972).

The questions of why there is SSD and why we perceive no major motion disruptions due to our rapid eye movements are two sides of the same coin. This question can also be framed as: "How and under which conditions does the visual system draw connections between the disconnected pre- and postsaccadic inputs?" For the "how" part of the question, research suggests that, instead of presaccadic information being overwritten or disregarded by the arrival of more reliable postsaccadic information, pre- and postsaccadic feature information can be integrated to form a single percept of increased precision, which is referred to as transsaccadic integration. It has been found that visual features such as orientation (Ganmor et al., 2015; Stewart & Schütz, 2018a; Stewart & Schütz, 2019a; Stewart & Schütz, 2019b; Wolf & Schütz, 2015), color (Schut, Van der Stoep, Fabius, & Van der Stigchel, 2018; Stewart & Schütz, 2018b; Wijdenes et al., 2015), and numerosity (Hübner & Schütz, 2017) are integrated and weighted by the reliability of each single input, resulting in the perception of the weighted sum that is more precise than the perception of each single input (Ernst & Bülthoff, 2004). Pre- and postsaccadic location information can also be integrated, which can aid target localization (Atsma, Maij, Koppen, Irwin, & Medendorp, 2016; Cicchini et al., 2013; Niemeier, Crawford, & Tweed, 2003; Prime et al., 2005; Vaziri, Diedrichsen, & Shadmehr, 2006; Zimmerman & Lappe, 2010). SSD can be considered to be the result of the integration of pre- and postsaccadic location information and as a result, a loss of access to the individual estimations (e.g., Niemeier et al., 2003).

However, transsaccadic feature integration is not necessarily an automatic process and may not occur without specific task demands (Stewart & Schütz, 2018b; Stewart & Schütz, 2019b; Stewart, Valsecchi & Schütz, in press); similarly, it is not mandatory for pre- and postsaccadic location information to be fully integrated. This leads to the "under which conditions" part of the above question. SSD can be explained in terms of two models that describe the conditions under which integration of pre- and postsaccadic location information occurs (Atsma et al., 2016; Niemeier et al., 2003). The first model posits that integration decreases as the discrepancy between pre- and postsaccadic location information increases, making perception of displacements more accurate (Niemeier et al., 2003). Specifically, Niemeier and colleagues suggested that the threshold after which integration declines may be determined by both a prior assumption of the visual system's intrinsic noisiness, and a prior assumption of extrinsic stability. Their model states that small discrepancies in pre- and postsaccadic location

information are attributed to internal noise, such as (unplanned) variability in saccade landing positions. The model predicts that the more uncertain a system is about its own sensorimotor state, the less likely it is to attribute displacements to an external cause.

The second model incorporates the two extreme assumptions about the world: Either the world is stable, which will lead to full integration, or it is not, which causes the inputs to be kept separate (Atsma et al., 2016). Evidence supporting either of these two options is weighted through a causal inference mechanism (Atsma et al., 2016; Körding, Beierholm, Ma, Quartz, Tenenbaum, & Shams, 2007; Wozny, Beierholm, & Shams, 2010). This model can also predict participant behavior and suggests similar conditions for SSD as the first model. However, Atsma et al. (2016) additionally showed that the strength of SSD increases with decreasing quality of location information obtained from an object, and their model can account for those effects by incorporating localization uncertainty as a factor influencing the stability assumption. Whereas Atsma et al. (2016) demonstrated that their model can explain more variability due to location information quality, the models by both Niemeier et al. (2003) and Atsma et al. (2016) suggest that increased SSD is due to increased sensory or sensorimotor uncertainty. Considering children as potential candidates for having increased sensory or sensorimotor uncertainty (see section on Development of saccadic suppression and information integration), both models make equivalent predictions that suggest stronger SSD in children.

SSD is a robust phenomenon, but it can also be disrupted. Deubel and colleagues found that blanking the saccade target for 50 to 300 ms immediately after the initial saccade seemed to reduce SSD (Deubel, Schneider, & Bridgeman, 1996). The authors named this decrease in displacement detection threshold the blanking effect. It might seem counterintuitive that making the target temporarily unavailable to the observer increases the likelihood of perceiving a displacement of the target; however, this effect can again be explained by a change in the assumption of external stability. The visual system might consider the disappearance of the saccade target upon landing as key evidence for a change in the world. That might strongly reduce, or even nullify a stability assumption, such that discrepancies in location information (e.g., due to a displacement of the saccade target) are assigned to external causes rather than internal noise; hence, thresholds for perceiving displacements are reduced (Deubel et al., 1996; Deubel, Bridgeman, & Schneider, 1998; Niemeier et al., 2003). Niemeier et al. (2003) were able to simulate the blanking effect by adjusting the stability assumption as a free parameter in their model. SSD is also reduced by other manipulations violating the stability assumption, such as task-irrelevant

orthogonal displacements (Wexler & Collins, 2014), contrast polarity, or object identity changes (Demeyer, Graef, Wagemans, & Verfaillie, 2010b; Tas, Moore, & Hollingworth, 2012).

A second view assigns the blanking effect to a change in the quality or processability of location information (Born, 2019; Ziesche, Bergelt, Deubel, & Hamker, 2017; Zimmermann, Morrone, & Burr, 2013). Specifically, the onset of the postsaccadic location information might convey critical evidence for a displacement (Born, 2019). Because postsaccadic blanking delays the onset of the postsaccadic location information to a time after saccadic suppression of contrast sensitivity, this information can be properly obtained in the blanking condition. This could mean then that either the quality of the location information is increased, leading to reduced SSD (Matsumiya, Sato, & Shioiri, 2016; but see Takano, Matsumiya, Tseng, Kuriki, Deubel, & Shioiri, 2020), or that enough time is provided for the visual system to fully process the location information (Ziesche et al., 2017). This second interpretation can explain SSD and blanking effects without the need for a stability assumption. However, it fails to explain several features of SSD: the elliptical window of SSD along the saccade trajectory (Wexler & Collins, 2014), the alleviation of SSD due to task-irrelevant feature changes (Demeyer et al., 2010b; Tas et al., 2012; Wexler & Collins, 2014), and illusory displacements that occur for a blanked target that appears adjacent to a target that was not blanked (Deubel, 2004; Deubel et al., 1998; Deubel, Koch, & Bridgeman, 2009; Higgins & Wang, 2009).

Given that current evidence from the literature is in favor of the explanation based on a violation of the stability assumption, a condition including a postsaccadic blank can serve as a measure of SSD when the stability assumption is rejected (Niemeier et al., 2003). This would substantially reduce the influence of sensory or sensorimotor uncertainty on SSD that might otherwise be higher in children compared to adults. What exactly can be expected from measuring SSD with and without a postsaccadic blank in children is evaluated in the following section.

Development of saccadic suppression and information integration

SSD and the blanking effect are robust phenomena that have been studied extensively in adults; however, we do not know whether children also experience these effects or when the potential mechanisms underlying these effects develop. Basic visual perception develops within the first few years of age (Braddick & Atkinson, 2011), but it is unclear when transsaccadic perceptual

processes develop in children; their development may rely more on the development of the oculomotor system than on the development of visual perception and may also reflect the greater variability in saccade execution that accompanies this development. The saccade planning system seems to still be developing up until around 8 years of age. Saccade latencies decrease with age (Bucci & Seassau, 2012; Cohen & Ross, 1977; Munoz et al., 1998; Salman et al., 2006) and reach the same level as adults by the age of 12 (Fukushima, Hatta, & Fukushima, 2000). Saccade gain seems to increase with age (Bucci & Seassau, 2012), with some studies indicating that children reach adult-like performance by the age of 8 (Munoz et al., 1998; Salman et al., 2006). This developing oculomotor control may result in greater uncertainty in saccade planning or execution. The models of Atsma et al. (2016) and Niemeier et al. (2003) would predict that this increased uncertainty may lead to greater SSD. Indeed, this seems to be the case for one such transsaccadic perceptual phenomenon, as saccadic suppression of contrast sensitivity is even more pronounced in children than in adults, with children showing three times more suppression than adults (Bruno, Brambati, Perani, & Morrone, 2006). This could be due to a stronger need to suppress information due to uncertainty in developing oculomotor functions (Bruno et al., 2006; Niemeier et al., 2003). If the development of SSD is similar to saccadic suppression of contrast sensitivity, then we would expect to see stronger SSD in children than adults. Studies on the development of multisensory integration may also give us insight as to when transsaccadic integrative processes may develop, because the integration of transsaccadic information and multisensory integration have been shown to rely on the same principles of optimal cue combination (Ganmor et al., 2015; Wolf & Schutz, 2015). Transsaccadic integration has not been studied in children; however, studies into the development of multisensory information suggest a rather late development. Nardini et al. (2008) showed that, while adults could optimally integrate and weight landmark and non-visual self-motion cues in a navigation task, children between 4 and 8 years of age failed to integrate the cues. Similarly, the integration of visuohaptic information develops only after the age of 8 to 10, before which children rely on a single modality (Gori et al., 2008). This late development may be due to the ongoing process of calibration to account for perceptual and sensorimotor development, or a failure to develop correspondence between different signals (Ernst, 2008; Gori et al., 2008). This latter idea was supported by Jovanovic & Drewing (2014), who found that children 6 years of age can integrate visuohaptic information, but only when the discrepancy between the stimuli was small, and when the stimuli were more likely to be attributed to a single origin. Calibration of perceptual and sensorimotor processes and causal correspondence

are both elements that may play a role in integrating pre- and postsaccadic position information (Atsma et al., 2016; Niemeier et al., 2003). The processes underlying transsaccadic information integration may also still be subject to a sensorimotor and perceptual calibration process in children. Integration of information during SSD may reflect integration processes involved in multisensory integration, in which case we would expect to see less integration of information and therefore less SSD in children than adults.

Rationale of this study

This study aimed to investigate the development of mechanisms supporting perceptual stability by comparing SSD and the blanking effect in children 7 to 12 years old and adults 19 to 25 years old. We aimed to make inferences about how SSD works by measuring a population in whom SSD has not yet fully developed. We measured SSD by displacing the saccade target during the saccade, with and without an intervening blank between the pre- and postsaccadic stimulus. The introduction of a postsaccadic blank allowed us to measure a reduction in SSD (Bridgemann et al., 1975); with the addition of the blank, we would expect that integration may also be reduced or may not occur. To further investigate the mechanisms underlying SSD, we related these perceptual measures to measures of oculomotor performance. Saccade landing accuracy and precision allowed us to determine the amount of uncertainty in saccade planning and execution, and corrective saccade latencies were used as a measure of internally predicted saccade error.

Methods

Participants

Seventeen adults and seventeen children who were unaware of the purpose of the study participated in the experiment. We excluded two adults: one who did not respond in accordance with the task, so psychometric functions were not well defined, and one who showed a strong bias to respond by saccade direction. Two children were excluded from analysis, both of whom responded by saccade direction, despite repeated attempts at instruction. Fifteen adults (11 females, four males; mean age 23 years, range 19–25 years) and 15 children (nine females, six males; mean age 9 years, range 7–12 years) were included for analysis (Figure 1B). The ages of the children were chosen based on multisensory integration literature, which suggests
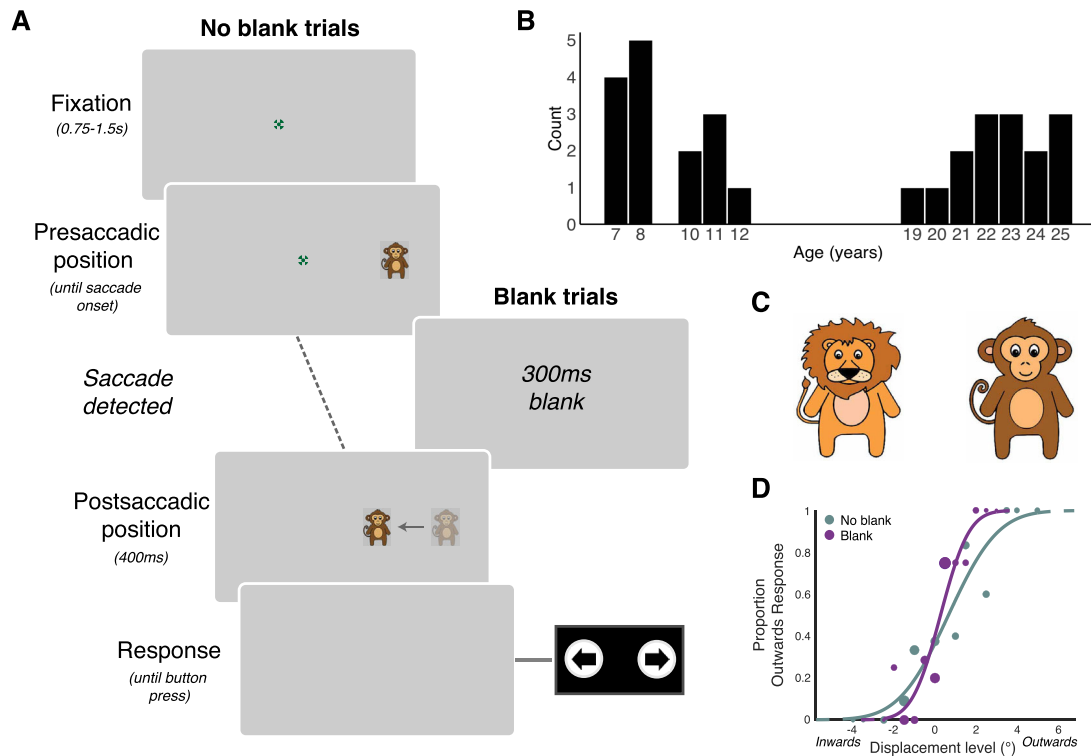
Figure 1. Experiment procedure and stimuli. (A) Trial sequence. Participants fixated a central fixation stimulus. Upon key press and after a random interval between 0.75 and 1.5 seconds, the target stimulus appeared at the presaccadic location. When the saccade was detected, the stimulus jumped either inward or outward either immediately (no-blank trials) or after 300 ms of blank screen (blank trials). Participants used a response box to indicate the direction of the jump. (B) Histogram of participant ages. (C) Monkey and lion stimuli. (D) Example psychometric functions for one participant (8 years old) showing fitted cumulative Gaussian distributions for blank (purple) and no-blank (turquoise) conditions.

that this range is interesting for the development of sensory calibration (Gori, 2015).

Adult participants were Marburg University students and were reimbursed for participation. Children were recruited via flyers inside and outside Marburg University and were accompanied by at least one legal guardian on the day of participation. Children were reimbursed with money and a toy of choice. The experiment was conducted in accordance with the tenets of the Declaration of Helsinki (1964) and approved by the local ethics committee of the Psychology Department at Marburg University (proposal number 2015-35k). All participants and their legal guardians in the case of the children gave informed consent. All participants had normal or corrected-to-normal vision.

Equipment

Stimuli were presented using a back-projection setup, using a PROPixx projector (VPixx Technologies, Saint Bruno, QC, Canada), with a resolution of 1920 × 1080 and a refresh rate of 120 Hz, projected onto a 91 × 51-cm screen from Stewart Filmscreen

(Torrance, CA). Viewing distance was 106 cm. The screen was calibrated to ensure a linear gamma correction and to correct the central hot spot, and it had a background luminance of 92 cd/m^2. The CIE 1931 *x*, *y* coordinates of the screen were (0.6722, 0.3222), (0.1707, 0.7390), and (0.1515, 0.0464) for red, green, and blue, respectively. Eye movements were recorded using an EyeLink 1000+ (SR Research Ltd., Kanata, ON, Canada), with a sampling rate of 1000 Hz. The experiment was presented with custom written software in MATLAB (National Institutes of Health, Bethesda, MD), using Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and the EyeLink Toolbox (Cornelissen et al., 2002). Participants responded using a Black Box Toolkit USB response pad (Black Box ToolKit Ltd., Sheffield, UK). All participants used a chin and forehead rest for head stabilization.

Eye tracker calibration

The eye tracker was calibrated using the participant's right eye for nine locations (marked by a fixation stimulus) in a grid array with one location at the center

of the screen and the remaining with an eccentricity of 17° of visual angle on the horizontal and/or 10° on the vertical axis. The experimenter confirmed gaze position at each location manually while ensuring that each difference between computed gaze position and stimulus location was below 0.75° of visual angle during validation. The calibration procedure was conducted before the start of the experiment and whenever the experimenter noticed that a participant needed a break (by verbal or nonverbal signals), which could be every 20 trials for the youngest participants. Despite children having to be reminded more frequently to restrain head and body movements, after successful instruction gaze position errors were about equal for children and adults across calibration procedures. In addition to the calibration procedure, at the start of each trial a drift check was implemented that was manually confirmed by the participant using the two lowest-positioned of four buttons on the response box.

Stimuli

The initial fixation stimulus was a combination of bull's-eye and crosshair, which has been demonstrated to be especially effective for maintaining stable fixation on a screen (Thaler, Schutz, Goodale, & Gegenfurtner, 2013). The fixation stimulus was 0.15° × 0.6° of visual angle. The color of the fixation stimulus was chosen randomly out of an array of colors generated in Derrington–Krauskopf–Lennie (DKL) color space (Derrington, Krauskopf, & Lennie, 1984), with randomized polarity and isoluminance toward the gray background to avoid the build-up of afterimages. Target stimuli were two animal cartoons designed to be appealing to the children in order to motivate them (Figure 1C). The monkey was 2.39° high and 1.76° wide. The lion was 2.51° high and 1.72° wide. Colors were chosen to match the animal and differed in luminance (Figure A4).

Procedure and design

The aim of our experiment was to measure SSD with and without a postsaccadic blank in children and adults. In order to get children interested in the experiment and sufficiently motivated to sit still through all trials, we first familiarized them with a jungle theme, and the subsequent task instructions were embedded in an imaginative role play where the child took on the role of a researcher investigating the jumping behavior of animals appearing in the jungle.

To start a trial, participants fixated a central fixation stimulus and simultaneously pressed a button on the response box. After a random interval varying between 0.75 and 1.5 seconds (during which time fixation was maintained), one of the animals appeared

at an 8° or 10° eccentricity, to either the left or right of central fixation (presaccadic target position) (Figure 1A). Applying an overlap paradigm (Saslow, 1967), the fixation stimulus remained on-screen with the presaccadic target and was removed either after an additional 200 ms following the fixation interval or when the presaccadic target was removed. The presaccadic target was removed as soon as the eye position exceeded 2° with respect to the screen center and reappeared either immediately (no-blank trial) or 300 ms later (blank trial) at the postsaccadic target location. The postsaccadic target location was shifted on the horizontal axis relative to the presaccadic target position by a magnitude and direction determined by an adaptive staircase procedure. This procedure was composed of three independent, randomly interleaved staircases for each condition, with a constant step size of 2.5° for the no-blank condition and 1.5° for the blank condition (per Ostendorf, Liebermann, & Ploner, 2010). The staircases started at an initial displacement level of 0°, –4° (left), and 4° (right) in the no-blank condition, or 0°, –2° (left), and 2° (right) in the blank condition. The step size was either added (rightward) or subtracted (leftward) from the current displacement level whenever a participant responded left or right perceived displacement, respectively. This procedure enabled us to measure the point of subjective stationarity and the just noticeable difference (JND) while keeping the total number of trials low.

The postsaccadic target was presented for a duration of 400 ms. The subsequent empty screen prompted the participant to respond whether they perceived a displacement direction to the left or to the right. Participants were told to guess when they did not perceive any displacement.

For motivation purposes, after every 10 trials, an illustration of a clipboard appeared indicating the number of animals observed thus far. Whenever a participant blinked within a trial, a sound of the animal running away was played together with a voice recording to remind the participant not to blink. When children were being tested, the experimenter remained inside the experimental room throughout the experiment and prompted a break every 30 trials, or whenever it seemed appropriate. Each participant completed at least 144 trials.

Analyses

Saccade onsets and offsets were detected offline using the EyeLink 1000+ algorithm (velocity threshold = 22°/s, acceleration threshold = 3800°/s^2). Saccade latencies of the main/initial saccades were defined as the first sample after target onset in which a saccade was detected; likewise, saccade offsets were defined as the last sample after saccade onset in which a saccade was

detected plus 10 ms (to bypass longer post-oscillation times). Corrective saccades were defined as saccades with onset at least 50 ms after initial saccade offset (no-blank trials) or 50 ms after postsaccadic stimulus appearance (blank trials). In addition, for a saccade to be considered a corrective saccade, the landing position had to be closer to the postsaccadic target position than the landing position of the initial saccade.

Trial exclusions

We excluded trials with erroneous saccades. These were defined as trials without any saccades, with saccades that were halted such that the displacement happened when the eye was stationary, with initial saccades directed opposite to target position, or with blinks occurring within 300 ms of target onset. We included all trials with saccade latencies between 50 and 1000 ms to account for the large variability in saccade latency within children (Munoz et al., 1998). The overall percentage of trial exclusions was 8% ± 7% for adults and 18% ± 11% for children (mean ± standard deviation), resulting in 142 ± 21 trials across all participants. Trial exclusions for each criterion and participant can be found in the Appendix (Tables A1 and A2).

Psychometric functions

To obtain psychometric functions (see example in Figure 1D), perceptual choices were converted into proportion outward responses for each displacement level tested (displacement levels were converted into inward/outward displacements with respect to screen center). A cumulative Gaussian was fitted to the data using the psignifit 4.0 toolbox for MATLAB (Schütt, Harmeling, Macke, & Wichmann, 2016). The point of subjective stationarity was estimated as the level of displacement corresponding to 50% outward responses. JNDs were defined as the standard deviation of the cumulative Gaussian, with lower JNDs indicating higher precision of displacement perception.

To assess the goodness of fit for each psychometric function we calculated the deviance (D) normalized by the number of displacement levels tested (listed in Tables A1 and A2). Deviance is a log-likelihood ratio between a saturated model and the fitted psychometric function and is recommended as a goodness-of-fit measure for binomial data (Schütt et al., 2016; Wichmann & Hill, 2001). To verify that fits were equally good for both blanking conditions, we performed a mixed analysis of variance (the assumption of normality was checked using a Lilliefors test, and the assumption of homogeneity of variance was checked using a Levene test) for the normalized deviances and found no significant effect for the within-factor blanking condition, $F(1, 28) = 0.37$, $p = 0.5486$; a

significant effect for the between-factor age group, $F(1, 28) = 12.24$, $p = 0.0016$; and no significant interaction between blanking condition and age group, $F(1, 28) = 2.39$, $p = 0.1333$. This confirms our expectation that psychometric function fits are less reliable for children, $D\_norm = 0.73 \pm 0.30$, than for adults, $D\_norm = 0.43 (0.34)$, due to a lower number of valid trials (also listed in Tables A1 and A2). However, as can be seen in Figures A1 and A2, even the psychometric functions for children achieved a reasonable fit. Most importantly, the reliability of fits did not differ between blank and no-blank conditions for either of the participant groups.

Statistical analyses

Linear models were calculated using R (R Foundation for Statistical Computing, Vienna, Austria) (based on Chambers, 1992; Wilkinson & Rogers, 1973). Linear mixed models were calculated in R using the nlme package (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2020). Pairwise comparisons were calculated in R using the emmeans package (Lenth, Buerkner, Herve, Love, Riebl, & Singmann, 2020). Bayes factors were calculated using the BayesFactor package in R (Morey, Rouder, Jamil, Urbanek, Forner, & Ly, 2019). For linear models, Bayes factors were calculated using the default inverse gamma prior. For linear mixed modes, Bayes factors were calculated using default priors (inverse gamma prior on the regression and Jeffreys prior on effects). Bayes factors for main effects were calculated as the ratio of evidence for the model containing only that factor versus the null (intercept and random effects only) model. Interactions were calculated as the full model with interaction term versus the model containing main effects with no interaction term. For t-tests, Bayes factors were calculated using default Jeffreys prior on variance and Cauchy prior on standardized effect size (Rouder, Speckman, Sun, Morey, & Iverson, 2009).

For linear models and linear mixed models, fixed effects of age group (children or adults) and blanking condition (blank or no-blank) were categorically coded, with children coded as baseline contrast factor level for age group comparisons and no blank coded as baseline contrast factor level for blanking condition comparisons. For mixed-model analyses, random effects structures are described in the results section. Assumptions of model fits (normality of residuals and homoscedascity) were checked using standard graphical procedures (Gelman & Hill, 2006; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We report statistics on the fixed effects of each model: F statistic, p value, and Bayes factors (BF_{10} indicates evidence against the null hypothesis). Statistical tests were performed on the data shown in the corresponding figures, such that there
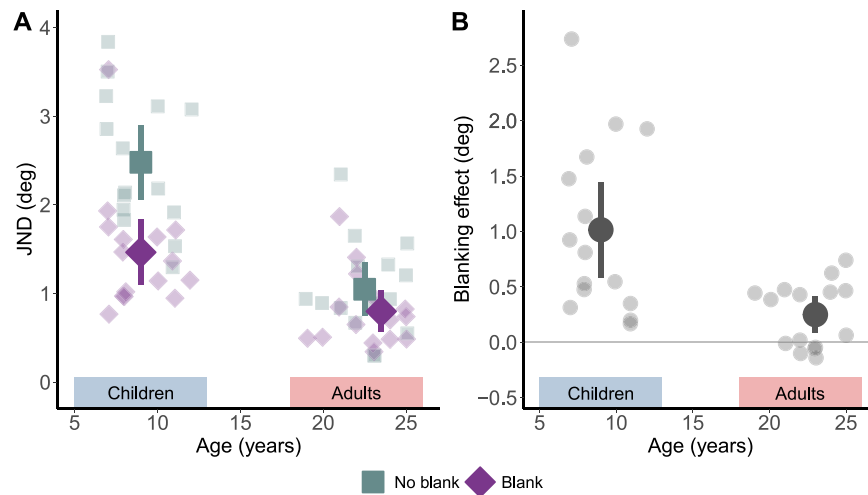
Figure 2. Perceptual performance. (A) JNDs for no-blank (turquoise squares) and blank (purple diamonds) conditions. (B) Blanking effect (difference between blank and no blank conditions). Individual subjects are shown by age in small symbols and means for children and adults in larger symbols (where mean symbols are offset on the *x*-axis to avoid overlap, they do not reflect mean age). Error bars are 95% CIs.

Results

Perceptual results

Saccadic suppression of displacement for children versus adults

To determine how JNDs changed across age and blanking condition (Figure 2A), we used a linear mixed model, with fixed effects of age group (children or adults) and blanking condition (blank or no blank), and random intercepts and slopes for blanking condition (blanking condition was nested within participant). There was a significant main effect of age group, $F(1, 28) = 28.76$, $p < 0.0001$, $BF_{10} = 931.07$ (extreme evidence), demonstrating that JNDs were lower for adults than for children, suggesting that SSD is stronger for children than adults (Figure 2). There was a significant main effect of blanking condition, indicating that JNDs differed significantly between blanking conditions across both age groups, $F(1, 28) = 34.6$, $p < 0.0001$, $BF_{10} = 607.95$ (extreme evidence). There was a significant interaction between blanking condition and age group, $F(1, 28) = 12.7$, $p = 0.013$, $BF_{10} = 18.91$ (strong evidence), suggesting that the difference between blank and no-blank conditions differed between children and adults. Post hoc pairwise

comparisons with a Holm correction for multiple comparisons showed a significant difference between blanking conditions for children: $t(28) = 6.68$, $p < 0.0001$.

Blanking effect for children versus adults

To further clarify how blanking affected SSD, we calculated the blanking effect as the difference in JNDs between blank and no-blank conditions (Figure 2B). This is essentially the same analysis as the interaction effect above; however it allows for a direct comparison of blanking effect with previous studies (Table A3). The mean blanking effect for adults was 0.25° (*SD* = 0.30°) and for children was 1.02° (*SD* = 0.78°). A linear model with fixed effect of age group showed a significant difference in blanking effect between children and adults, $F(1, 28) = 12.7$, $p = 0.0013$, $BF_{10} = 24.44$ (strong evidence), demonstrating that children had a larger blanking effect than adults. To ensure that this was not due to the relative difference in absolute JND levels between children and adults, we also compared the relative blanking effect for the two age groups. The relative blanking effect was calculated for each participant as the *difference* in JND between blank and no-blank conditions for that participant, divided by the *mean* of the blank and no-blank JND for the participant: $(JND_{Blank} - JND_{NoBlank})/[(JND_{Blank} + JND_{NoBlank})/2]$. The difference between children and adults was again still significant, $F(1, 28) = 4.93$, $p = 0.035$, $BF_{10} = 2.06$ (anecdotal evidence), showing that children had a larger blanking effect than adults.
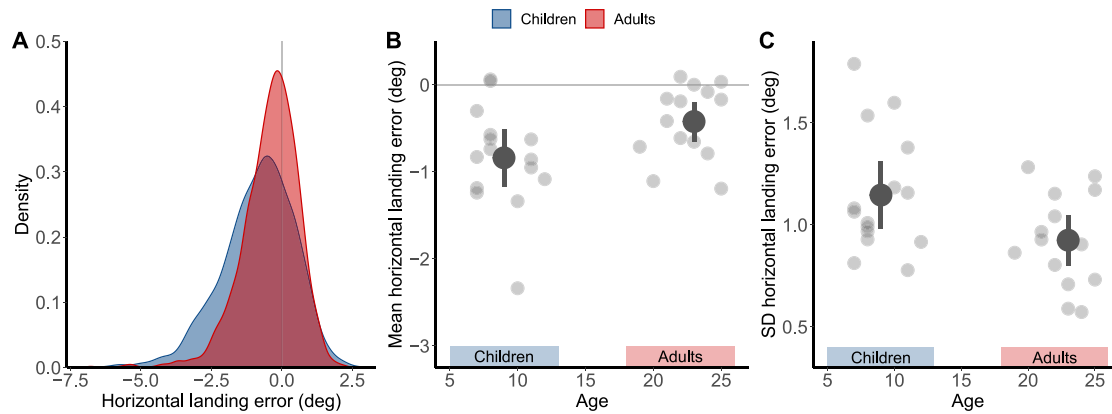
Figure 3. Horizontal landing error for children (blue) and adults (red). (A) Horizontal landing error (negative values represent undershoot of target), as density distributions. (B) Mean horizontal landing error by age. (C) SD horizontal landing error by age. In (B) and (C), small gray symbols represent individual subjects, and large symbols represent mean values for children (blue) and adults (red). Error bars are 95% CIs.

	Mean (SD), °		Median (IQR), ms	
	Horizontal landing error – initial saccade	Vertical landing error – initial saccade	Initial saccade latency	Corrective saccade
Children				
No blank	−0.87 (1.1)	−0.19 (0.49)	191.1 (134.8)	150.7 (54)
Blank	−0.80 (1.2)	−0.18 (0.48)	182.5 (142.5)	180.6 (92.8)
Adults				
No blank	−0.41 (0.93)	−0.15 (0.35)	161.5 (78)	199.5 (84.9)
Blank	−0.43 (0.92)	−0.14 (0.34)	163.2 (83)	213.2 (85.6)

Table 1. Summary saccade metrics. Mean and standard deviation landing error and median and interquartile range (IQR) initial and corrective saccade latency are reported.

Eye movement results

Accuracy and precision of initial saccades

Given that the SSD may be related to the precision and accuracy of saccades in the direction of displacement (Wexler & Collins, 2014), we examined how horizontal landing error for the initial saccade differed across age (Figures 3A and 3B; Table 1). We compared saccade accuracy (mean horizontal landing error) between age groups (children or adults) with a linear model. There was a significant effect of age group, $F(1, 28) = 5.05$, $p = 0.033$, $BF_{10} = 2.14$ (anecdotal evidence). Both groups showed an undershoot of the saccade target; a one-tailed *t*-test showed that mean horizontal landing position was significantly different from 0 (the directional *t*-test was used to compare whether the mean was less than 0). For children, $t(14) = -5.48$, $p < 0.0001$, BF_{10} (evidence mean < 0/evidence mean not < 0) = 24815.96 (extreme evidence). For adults, $t(14) = -4$, $p = 0.0007$, BF_{10} (evidence mean < 0/evidence mean not < 0) = 803.1 (extreme

evidence). Children showed on average a larger undershoot than adults. Similarly, we compared saccade precision (variability in horizontal landing error), showing a significant decrease with age group, $F(1, 28) = 5.26$, $p = 0.029$, $BF_{10} = 2.31$ (anecdotal evidence). This suggests that initial saccade accuracy and precision were greater in adults than children.

Saccade accuracy and blanking effect

To test whether saccade accuracy was related to the magnitude of the blanking effect, we used a linear model to test whether horizontal landing error in the no-blank condition was predictive of the magnitude of blanking effect (blanking effect as a function of log horizontal landing error to correct the assumption of normally distributed residuals). There was a significant relationship between horizontal landing error and blanking effect, $F(1, 28) = 8.93$, $p = 0.0058$, $BF_{10} = 7.71$ (moderate evidence). This suggests that as
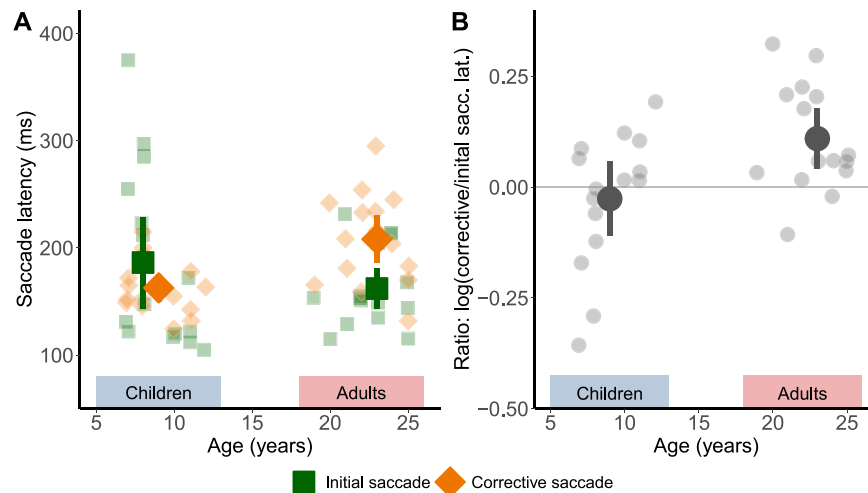
Figure 4. Initial versus corrective saccade latencies. (A) Initial (green squares) and corrective (orange diamonds) saccade latencies by age. (B) Log ratio of corrective to initial latencies by age. The ratio is calculated as the log of corrective latency divided by initial saccade latency. In (A) and (B), individual subjects are shown by age in small symbols and means for children and adults in larger symbols (mean symbols are offset on the *x*-axis to avoid overlap and do not reflect mean age). Error bars are 95% CIs.

saccade accuracy decreased the amount of postsaccadic target displacement tolerated increased.

Shared noise in perception and eye movements

We based our analysis on the assumption that expectations of internally caused errors are intrinsic to a participant, rely on long-term experience, and would not change on a trial-by-trial basis. It is, however, entirely possible that perceptual performance also correlates with motor performance on a given trial—for example, due to shared noise sources (Stone & Krauzlis, 2003; Liston & Stone, 2008; but see Gegenfurtner, Xing, Scott, & Hawken, 2003). In other words, high internal noise on a given trial might affect both perception of displacement and saccade landing error. To determine to what extent a correct or incorrect perceptual response can be predicted based on the horizontal landing error of the initial saccade, we conducted a receiver operating characteristic (ROC) curve analysis over all blank and no-blank trials that could be labeled as correct or incorrect based on response and displacement direction (zero-displacement trials were discarded). We calculated the areas under the ROC curves (AUCs) with a baseline of 0.5 (AUC values above the baseline indicate a predictability above chance). For children (no blank = 0.56, blank = 0.55) and for adults (no blank = 0.57, blank = 0.53), horizontal landing error could marginally predict response correctness with slightly higher predictability for the no-blank condition. While we think that this analysis points to a limited contribution of shared noise to perceptual and motor performance, the relatively small AUC values do not contradict the assumption of experience-based

expectations as being the main cause for the blanking effect difference between children and adults.

Initial and corrective saccade latencies

Previous studies have shown that both initial and corrective saccade latencies decrease as children become older (Cohen & Ross, 1978; Munoz et al., 1998; Salman et al., 2006). To see if this was also the case in this study, we compared initial and corrective saccade latencies across age (Figure 4A; Table 1). We used a linear mixed-effects model, with fixed effects of age group (children or adults), saccade type (initial or corrective saccade), and blanking condition (blank or no-blank), and random intercepts and slopes for subjects (blanking condition nested within subject). Saccade latency was log-transformed to meet the assumption of normality of residuals for the test (Gelman & Hill, 2006). There was no significant main effect of age group, $F(1, 28) = 0.78$, $p = 0.39$, $BF_{10} = 0.44$ (anecdotal evidence for the null hypothesis), indicating that overall saccade latencies did not differ by age. There was a significant main effect of saccade type (initial vs. corrective saccade), $F(1, 56) = 5.9$, $p = 0.019$, $BF_{10} = 1.76$ (anecdotal evidence), indicating that initial and corrective saccade latencies differed across all age groups and blanking conditions. There was no significant main effect of blanking condition, $F(1, 28) = 2.04$, $p = 0.16$, $BF_{10} = 0.39$ (anecdotal evidence for the null hypothesis), indicating that overall latencies did not differ between blanking conditions. There was, however, a significant interaction between saccade type and age, $F(1, 56) = 14.3$, $p = 0.0004$, $BF_{10} = 87.9$ (very strong evidence), suggesting that

across both blanking conditions the difference between initial and corrective saccade latencies differs by age. Post hoc multiple comparisons with a Holm correction demonstrate a significant difference between saccade type for adults, $t(56) = -4.39$, $p = 0.0001$, but not for children, $t(56) = 0.96$, $p = 0.34$. There was no significant interaction effect between saccade type and blanking condition, $F(1, 56) = 2.66$, $p = 0.11$, $BF_{10} = 0.66$ (anecdotal evidence for the null hypothesis), or among age group, saccade type, and blanking condition, $F(1, 56) = 0.82$, $p = 0.37$; however, $BF_{10} = 9.41$ provides moderate evidence for an interaction.

To further investigate the relationship between initial and corrective saccade latencies, we calculated the log ratio of corrective saccade latency and initial saccade latency for each participant (Figure 4B). The log value was used to place ratio values below and above 1 on the same scale. We compared this log ratio between the two age groups (children and adults). A linear model showed a significant difference between the groups, $F(1, 28) = 7.22$, $p = 0.012$, $BF_{10} = 4.44$ (moderate evidence). This indicates that this ratio changed across age; relative to adults, younger participants had shorter corrective saccade latencies relative to their initial saccades. Specifically, although older adults had longer corrective than initial saccade latencies, initial and corrective saccade latencies for children did not differ. This suggests that children were faster to execute a corrective saccade compared to adults. Although on average corrective and initial saccade latencies did not differ for children, seven out of 14 children were even able to execute corrective saccades at latencies shorter than their initial saccades.

Corrective saccade latencies versus landing error

Previous studies have shown that the latency of corrective saccades depends on the magnitude of error after the initial saccades (Becker, 1972; Kapoula & Robinson, 1986; Lisi, Solomon, & Morgan, 2019; Ohl, Brandt, & Kliegl, 2011; Ohl, Brandt, & Kliegl, 2013). Hence, the shorter latencies of corrective saccades in children might be a mere consequence of their more variable landing errors in initial saccades (Figure 3; Table 1). If children have a higher predicted landing error due to more variability in saccade execution or planning, they should be faster to execute a corrective saccade to rectify this predicted error.

To test this hypothesis, we next looked at the relationship between corrective saccade latencies and horizontal landing error. For this analysis, landing error was calculated as horizontal distance between initial saccade landing position and postsaccadic stimulus position. Negative errors indicate an undershoot followed by an outward corrective saccade, and positive

errors indicate an overshoot followed by an inward corrective saccade (Figure 5C).

To compare differences between children and adults, we calculated mean corrective saccade latencies separately for undershoots and overshoots of initial saccades, corresponding to outward or inward corrective saccades, respectively (Figure 5, diagram; gray panels). For each blanking condition, we compared groups using a linear mixed model with fixed effect of age group (adults or children) and initial saccade error direction (undershoot or overshoot), and random intercepts for participant. For the no-blank condition, there was a significant effect of age group, $F(1, 28) = 15.96$, $p = 0.0004$; $BF_{10} = 42.9$ (very strong evidence), and initial saccade error direction, $F(1, 27) = 13.63$, $p = 0.001$, $BF_{10} = 15.85$ (strong evidence), as well as a significant interaction between age group and initial saccade error direction, $F(1, 27) = 8.66$, $p = 0.0066$, $BF_{10} = 4.9$ (moderate evidence). Post hoc multiple comparisons with a Holm correction showed a significant difference between undershoots and overshoots for children, $t(27) = 4.64$, $p = 0.0002$, but not for adults, $t(27) = 0.54$, $p = 0.59$. For the blank condition, there was a significant effect of age group, $F(1, 28) = 8.07$, $p = 0.0083$, $BF_{10} = 3.79$ (moderate evidence), but not of initial saccade error direction, $F(1, 28) = 3.31$, $p = 0.08$, $BF_{10} = 1.17$ (anecdotal evidence), or interaction between age group and initial saccade error direction, $F(1, 28) = 0.016$, $p = 0.9$, $BF_{10} = 0.32$ (moderate evidence for the null hypothesis). These results suggest that children made faster corrective saccades than adults for undershoots rather than overshoots, but this only seemed to occur in the no-blank condition. We outline potential explanations for this difference in the Discussion section.

Discussion

This study investigated how blanking affects SSD in children 7 to 12 years of age and adults. The results showed that in the no-blank condition children had overall larger JNDs than adults (i.e., greater SSD). Children also showed a larger blanking effect (improvement in JND from the no-blank to the blank condition) than adults. Measures of saccade dynamics show that initial saccades were more variable and had a larger undershoot in children. At the same time, children had shorter corrective saccade latencies than adults, especially when the initial saccade undershoots the postsaccadic target. Taken together, these results suggest that, compared to adults, children tolerate larger intrasaccadic displacements, thereby perceiving the stimulus as stationary. This may be due to a greater internal expectation or prediction of any discrepancy between pre- and postsaccadic location information
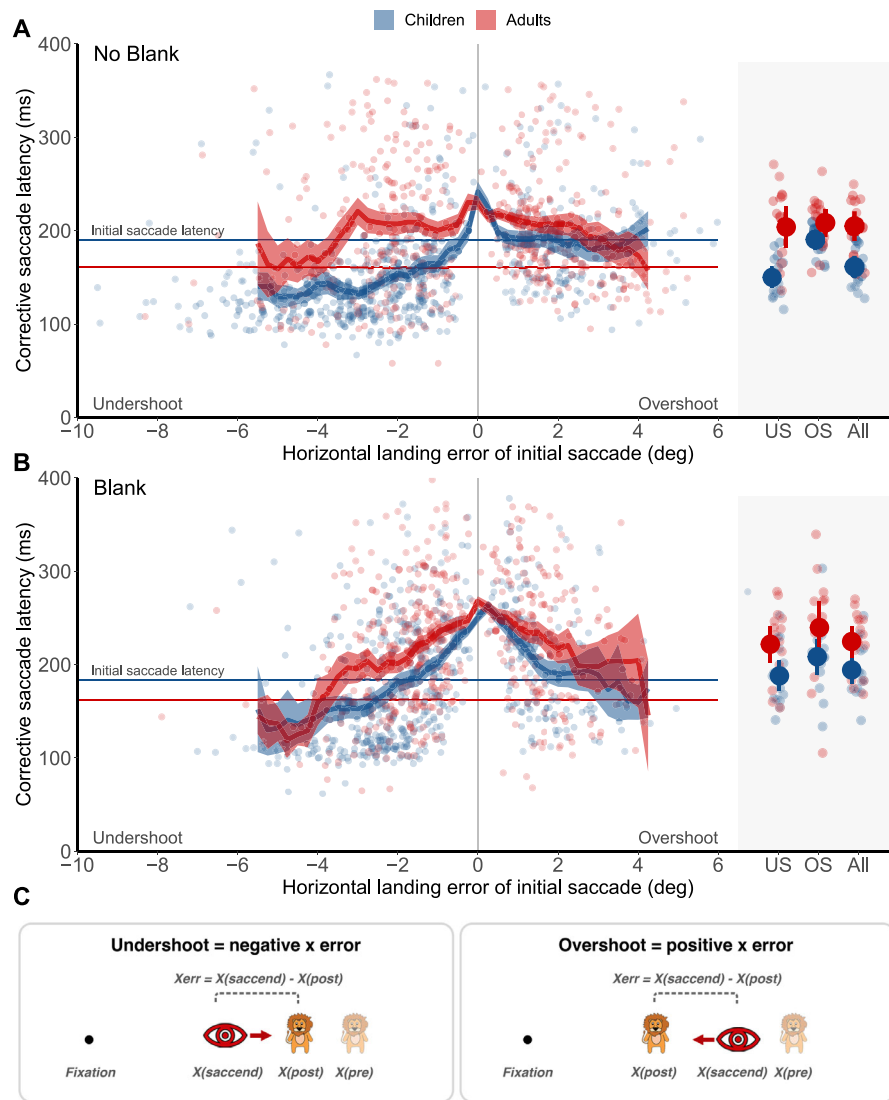
Figure 5. Landing error (initial saccade endpoint to postsaccadic stimulus) versus corrective saccade latency for no-blank trials (A) or blank trials (B). Points in the white panels are individual saccade latencies for all subjects; ribbon plots represent a moving average of saccade latencies for all participants across the range of landing errors (average latencies were calculated in a moving window ranging from −5.75 to 4.25 in steps of 0.25°, with a window size of 0.5°). Small symbols in the gray panels indicate mean saccade latencies for individual subjects grouped by undershoot (US) or overshoot (OS), or both (All); large symbols represent mean saccade latencies across all participants. All error bars are 95% CIs. Adults are represented with red markers, children with blue. (C) Examples to illustrate *x*-axis landing error calculation for corrective saccades for undershoots and overshoots, showing the pre- and postsaccadic positions of the stimulus, initial saccade landing position, and direction of the corrective saccade (red arrow).

being self-induced due to greater or more variable motor error or target localization error.

SSD and greater movement variability in children

Perhaps the most parsimonious explanation for why children showed greater SSD than adults is that they have a larger uncertainty about their saccade landing position relative to the target (saccadic uncertainty). The models of Niemeier et al. (2003) and Atsma et al. (2016) both predict that stronger SSD is due to increased internally caused uncertainty. A larger saccadic uncertainty in children may result in a larger tolerance for intrasaccadic position changes (Niemeier et al., 2003). This is evidenced by two factors in our data: children had more variable initial saccade landing errors and faster corrective saccade latencies. Variability

in saccade gain decreases with age (Bucci & Seassau, 2012; Munoz et al., 1998; Salman et al., 2006), and we saw that the children in this study also had greater horizontal landing variability than the adult group (Figure 3). Wexler and Collins (2014) suggested that there is an elliptical zone around the saccade endpoint in which stimulus displacements are not noticed; this region reflects the variance of saccade landing positions. Given that children have more variability in horizontal landing error, they may be more likely to have a larger "window" of tolerance for intrasaccadic displacements. In terms of SSD, this means that larger displacements will be tolerated than in adults, who have smaller variability in saccade landing error.

The second line of evidence comes from faster corrective saccades in children. If children have a higher internal expectation or prediction of an inaccurate saccade, they should be faster to execute a corrective saccade to account for this predicted error. Note that expectation in this sense is not a conscious expectation but rather an internal prediction of greater motor error by the oculomotor system. As Figure 4 shows, children are faster to execute corrective saccades than adults even at similar error sizes, and this is especially the case when the corrective saccade is made to correct an undershoot of the initial saccade. Saccades are typically hypometric (Becker, 1989), and this is also the case in children, although children additionally have greater variability in their saccade gain (Munoz et al., 1998; Salman et al., 2006) (and see Figure 3). In trials where the initial saccade undershoots both the pre- and postsaccadic stimulus location (Figure 5C), there could be a high internal expectation for the discrepancy between landing position and target location, as this would automatically be attributed to the natural high variability in saccade undershoot. Hence, a corrective saccade is rapidly executed. In the case where the initial saccade overshoots the postsaccadic target position, the discrepancy in pre- and postsaccadic stimulus location may be less expected (as saccade overshoots are less common), thus corrective saccade latencies are slower. Interestingly, this effect is more prominent in the no-blank condition. This may be due to the fact that, in the no-blank condition, the anticipated corrective saccade can be executed immediately as the postsaccadic target information is available upon landing, whereas in the blank condition the target is not available directly after the saccade (Tian, Ying, & Zee, 2013). The corrective saccades in the blank condition are more likely to be reactive saccades in response to the reappearing target, which are independent from the high expectation of having to correct an inaccurate initial saccade.

Shorter corrective saccade latencies and greater landing variability in children seem to suggest that children are more variable in their saccade execution and have a greater internal expectation of saccadic

error. This would adhere to the framework of Atsma et al. (2016) and Niemeier et al. (2003) regarding greater SSD being caused by increased intrinsic uncertainty. Although Atsma et al. (2016) considered localization uncertainty to be one potential source of uncertainty, Niemeier et al. (2003) referred to saccade landing variability. While they ostensibly refer to different processes, it is possible that saccade landing variability inherently reflects the inability to localize the peripheral target accurately (Lisi et al., 2019). It has been suggested that the major component causing saccade landing variability is uncertainty in peripheral target localization and that noise in motor commands explains only a small fraction of the variability (van Beers, 2007), however that study focused on adults, and the relative contribution of motor noise may be higher in children with a less well-calibrated oculomotor system. We cannot dissociate whether, in this current study, the variability in landing position for children came from more noise in motor execution compared to adults or was due to greater uncertainty in peripheral target localization. Different parameters associated with saccade execution develop at different times. Peak velocity and accuracy develop faster than saccade latencies and fixation control (Munoz et al., 1998; Salman et al., 2006), suggesting that structures controlling saccade execution located in the brainstem and cerebellum (Leigh & Zee, 1991; Wurtz & Goldberg, 1989) may develop earlier than cortical structures controlling saccade programming in the parietal and frontal networks, as frontal regions do not reach maturity until late adolescence (Anokhin, Birbaumer, Lutzenberger, Nikolaev, & Vogel, 1996; Thatcher, Walker, & Giudice, 1987). This may point to increased uncertainty in localization in children compared to adults, but we cannot confidently make any conclusions based on the current data.

While the assumption of greater internal uncertainty in saccade planning may be our favored hypothesis to explain these results, there are a number of other, non-mutually exclusive potential explanations. One mechanism related to SSD is saccadic suppression of contrast sensitivity, and children have been shown to have over three times greater saccadic suppression of contrast sensitivity than adults (Bruno et al., 2006). Our observed results of greater SSD in children could be due to greater suppression in general during the saccade.

Furthermore, increased SSD in children could also be due to temporal factors. Research suggests that there is a specific postsaccadic spatiotemporal window where the system determines whether stimuli surrounding the saccade endpoint are the same as the presaccadic stimuli (Deubel et al., 1998). It could therefore also be the case that this temporal window is widened, due to greater uncertainty about when they are executing a saccade. If children are unable to segregate stimulus information

into pre- or postsaccadic categories, they would not be able to accurately calculate intrasaccadic position changes; however, we think that this explanation is less likely, as a number of studies suggest that temporal integration windows in children do not differ from adults (Arnett & di Lollo, 1979; Hogben, Rodino, Clark, & Pratt, 1995) and, more importantly, that children are also able to segment temporal information as well as adults by the age of 5 (Freschl, Melcher, Kaldy, & Blaser, 2019).

An alternative explanation for larger JNDs in children is that children might have more unintentional errors or a greater fluctuation in attention rather than stronger SSD. Although it is probable that children's data are inherently more noisy than those of adults, we would expect that this would affect blank and no-blank conditions alike, resulting in a similar blanking effect as in adults. This is supported by the observation that the quality of the psychometric function fits was similar in the blank and the no-blank condition. Therefore, we think it is unlikely that the difference in SSD and the blanking effect between children and adults is caused by inattention in children.

Blanking effect and the development of integration in children

In this study, we observed that introducing a blank between the pre- and postsaccadic stimulus reduced SSD, and this blanking effect was even larger for children than for adults. These results provide an insight into how mechanisms of integration and segregation may develop in children. The increased SSD for children suggests that unisensory integration mechanisms may be developed in even the youngest participants (7 years old). Although this may at first glance be in contradiction with studies of the development of multisensory integration which suggest that *less* integration occurs due to an ongoing perceptual and oculomotor calibration process (Ernst, 2008; Gori et al., 2008), the same underlying principle could apply. Here, we saw that children showed more SSD, so potentially more integration of pre- and postsaccadic position information than adults. We can speculate that children are still calibrating how discrepancies in pre- and postsaccadic position error relate to their own saccadic accuracy, and the narrowing spatial window of integration with age reflects this ongoing calibration process. This calibration process may be crucial for the visual system to learn its own motor errors; as the visuomotor system develops, it must learn when transsaccadic position changes can be attributed to either internal factors (i.e., motor error or localization uncertainty) or external factors, such as a physical position change. If position discrepancies are falsely

attributed to external factors early in development, then the oculomotor system would never learn its own errors. If it assumes (as may be evident from this study) more error from its own noisy localization and execution, it can learn to correct these errors.

Indeed, feedback has been shown to be vital in the development of sensory integration and calibration; children can learn to integrate sensory cues only when they receive feedback about their judgments (Negen et al., 2019), and delaying feedback inhibits sensorimotor recalibration in children (Vercillo, Burr, Sandini, & Gori, 2015). Also, and in comparison to the multisensory development literature, many studies have shown that the ability to integrate and segment basic visual features, motion, and patterns develops very early in life (for review, see Braddick & Atkinson, 2011). This multi-stage development of integration mechanisms may reflect both the complexity of the information being integrated and ongoing physical development. It may be unsurprising that basic visual feature integration develops early, as the basic architecture of the visual system matures within the first few years of life (Braddick & Atkinson, 2011). Integration of different visual features such as stereo and motion or texture, which has been found to occur in adults (Johnston, Cumming, & Landy, 1994; Knill & Saunders, 2003), may be slower to develop, as depth processing is calibrated to account for the changing position of the eyes in a growing head, in a manner similar to how integration of visuohaptic information relies on the calibration of the developing haptic system (Ernst, 2008; Gori et al., 2008). Adults can learn novel cue combination within a few hours (Negen, Wen, Thaler, & Nardini, 2018), suggesting that the slow development of multisensory cue combination may be limited by biological development (Negen et al., 2019).

A caveat to this discussion, however, is that we cannot say for certain whether increased SSD is caused by an increase in integration per se or whether it is rather a failure to segregate. While models such as those posited by Atsma et al. (2016) and Niemeier et al. (2003) may predict a dichotomous relationship between integration and segregation, this may be an oversimplification of a more nuanced set of processes, and the finding that children do not segregate pre- and postsaccadic information does not mean that they necessarily integrate it. As such, and while this study provides insight into the development of SSD and transsaccadic location integration, we are hesitant to draw conclusions about the generalizability of these results to other potentially related measures of transsaccadic integration. It may be the case that these results do reflect a well-developed transsaccadic integration mechanism in children, and this may extend to integration of feature information such as orientation and color, as well as location information. Whether this integration would be near-optimal, as it is

in adults (Ganmor et al., 2015; Wolf & Schütz, 2015), is unclear. A likely scenario is that integration occurs; however, as with multisensory integration (Ernst, 2008; Gori et al., 2008), until the calibration of oculomotor systems is complete this integration may be suboptimal.

In children, as in adults, the intervening blank decreased SSD. The Atsma et al. (2016), and Niemeier et al. (2003) models predict that, when a blank is introduced, the stimuli should be segregated rather than integrated; the decreased JNDs in the blank condition compared to no-blank condition for both children and adults are in accordance with this hypothesis. The introduction of a blank provides an additional cue that the intrasaccadic position change may be due to a change in the environment. When the world is no longer assumed to be stable, any discrepancies between pre- and postsaccadic positions can be attributed to a change in the world, rather than internal uncertainty (Niemeier et al., 2003). These results also suggest that the assumption of a stable visual world may have developed by the age of 7, which may not be surprising, as this is a core mechanism underpinning transsaccadic perceptual stability.

It should also be noted that the magnitude of the blanking effect observed in this study was relatively small for adults compared to some previous studies (Table A3). One possible explanation is that the blanking effect has been shown to decrease with decreasing luminance contrast and for isoluminant color (Matsumiya et al., 2016; Takano et al., 2020), and, although our stimuli are far from low luminance contrast, the small blanking effect for adults might be explained by the strong color contrast in our stimuli, which were designed primarily to be appealing to children. Interestingly, these results are similar to those of Tas et al. (2012), who found a smaller blanking effect for colored, real-world stimuli compared to the typically utilized monochrome black disk stimulus (Table A3). While investigating the role of stimulus properties on blanking was not a goal of this study, it is interesting to note that these results, taken together with those of Tas et al. (2012), indicate that the blanking effect may be reduced for colorful, complex stimuli.

Initial saccade latencies

In accordance with previous studies, initial saccade latencies were shorter for adults than children; however, the initial saccade latencies for children in this study are considerably shorter than those previously reported (Table A4). This could be due to discrepancies in the stimuli used; while previous studies utilized a monochrome point or square target, our targets were specifically designed to be interesting for children and were embedded in an exciting narrative. Cohen & Ross (1977, 1978) found that when children were

given a "warning" signal 300 ms before the saccade, saccade latencies reflected those of adults, suggesting that processing limitations are not necessarily the cause of longer latencies in children, and higher level factors could be responsible instead. In adults, it has been shown that saccade latencies can be reduced by about 35 ms if the saccade target is associated with a perceptual task (Bieg, Bresciani, Bülthoff, & Chuang, 2012; Guyader, Malsert, & Marendaz, 2010; Montagnini & Chelazzi, 2005; Trottier & Pratt, 2005; Wolf & Schütz, 2017). It is possible that the saccade latencies in children may depend more on motivational aspects and that their facilitation by an engaging task is even larger than in adults. Because our task was designed to be especially motivating for the children, we can be sure that our young participants were paying attention to the task. The remaining delay in initial saccade latency compared to adults might be due to increased localization uncertainty, which may result in a longer processing time (Carpenter, 2004; Collins, 2016; van Loon & Adam, 2006; Zimmermann et al., 2013); this would be in accordance with the increased intrinsic uncertainty assumption.

Postsaccadic presentation duration

One noteworthy methodological difference between this and previous studies on SSD and blanking effects concerns the presentation duration of the postsaccadic target. While we used a fixed presentation duration of 400 ms for the postsaccadic stimulus, all other studies listed in Table A3 varied the duration depending on participant response time, which is presumably in the range of 500 to 1000 ms after saccade landing. Hence, it can be assumed that we provided less time for encoding the postsaccadic target location compared to previous studies, and one might argue that this affected the strength of SSD. However, we think that this was not the case for two reasons. First, the postsaccadic target duration was sufficiently long to allow for the execution of corrective saccades that were directed at the new postsaccadic location of the target (Figure A3); hence, the information about the new postsaccadic target location was already available and processed in the oculomotor system. Second, the mean JNDs of adults in the no-blank condition were well within the range of reports in the literature, suggesting that our paradigm produced typical SSD.

Conclusions

This study keep showed that children 7 to 12 years old experience greater saccadic suppression of displacement than adults and additionally show a greater blanking effect than adults. Children had larger undershoots and

more variability in their initial saccades than adults and were faster to execute corrective saccades in response to these undershoots. Taken together, these results suggest that children have a greater expectation for inaccurate saccades and therefore have greater tolerance for discrepancies in pre- and postsaccadic stimulus position.

Keywords: saccade, transsaccadic, children, blanking, saccadic suppression of displacement

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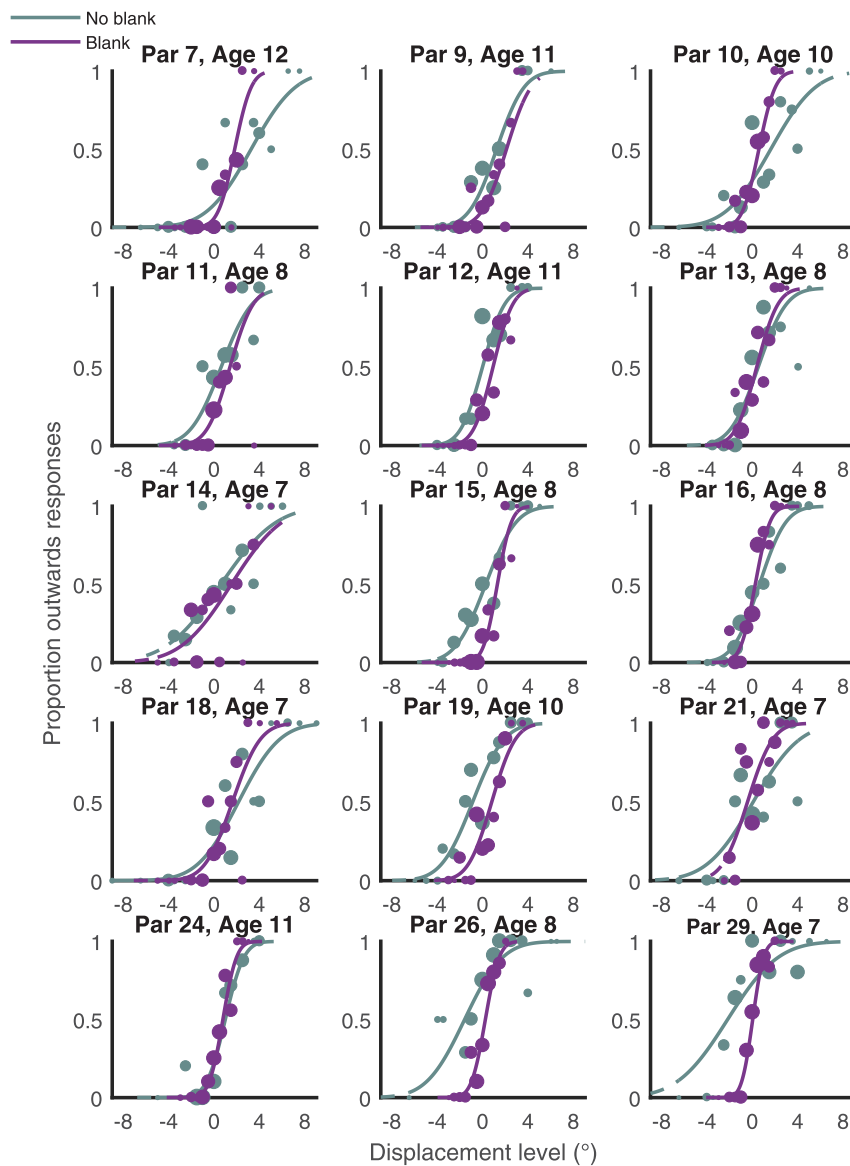
Appendix

Figure A1. Psychometric functions for all children showing fitted cumulative Gaussian distributions for blank (purple) and no-blank (turquoise) conditions.
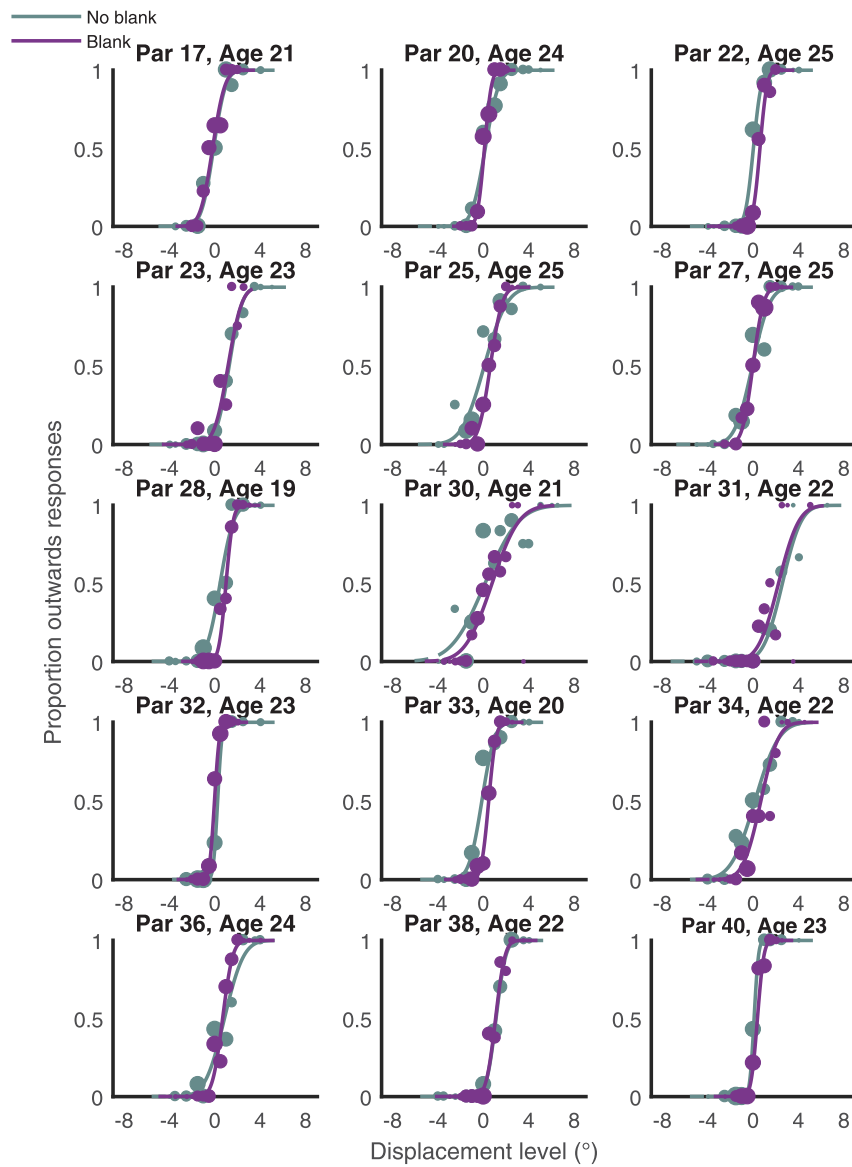
Figure A2. Psychometric functions for all adults showing fitted cumulative Gaussian distributions for blank (purple) and no-blank (turquoise) conditions.
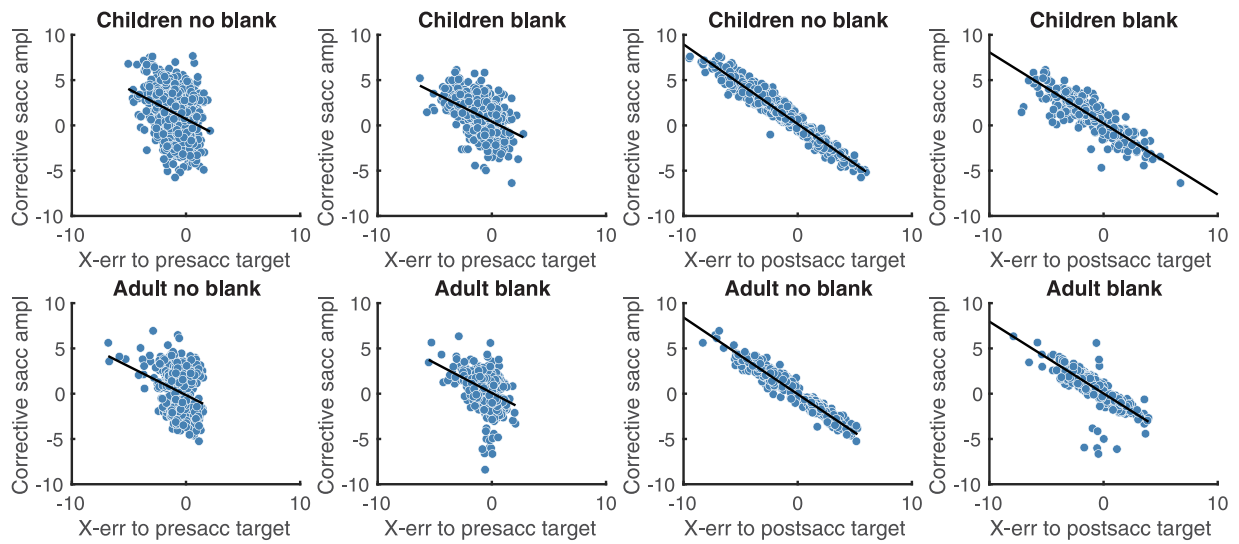
Figure A3. Correlation between corrective saccade amplitude and horizontal landing error to pre- or postsaccadic target position. Correlation coefficients for amplitude versus presaccadic target position: children no-blank, –0.33; children blank, –0.46; adult no-blank, –0.31; adult blank, –0.38. Correlation coefficients for amplitude versus postsaccadic target position: children no-blank, –0.97; children blank, –0.89; adult no-blank, –0.97; adult blank, –0.84.

Figure A4. Lion and monkey stimuli with RGB values on a gray (128, 128, 128) background.

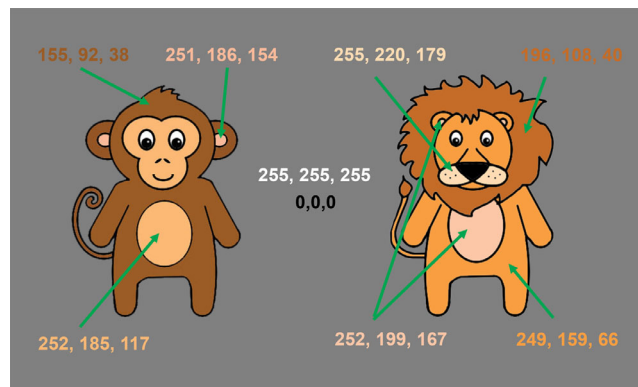| Child participant number	Age (y)	Erroneous saccades (n)	Saccade latency	Total number of exclusions	Total number of valid trials; total number of trials	Mean (SD) Number of trials per displacement level in no-blank condition	Number of trials per displacement level in blank condition	Normalized deviance no-blank; blank
7	12	22	18	40	104; 144	3.63 (1.96)	3.54 (2.79)	0.89; 0.37
9	11	27	0	27	117; 144	4.67 (2.5)	3.81 (2.4)	0.49; 0.71
10	10	11	0	11	133; 144	4.64 (2.53)	5.67 (3.28)	0.93; 0.42
11	8	32	20	52	92; 144	4.5 (1.84)	3.92 (2.39)	0.7; 1.05
12	11	11	3	14	130; 144	5.91 (3.18)	4.33 (3.04)	0.71; 0.39
13	8	11	12	23	121; 144	5.36 (3.11)	4.77 (3.3)	1.06; 0.6
14	7	37	0	37	107; 144	4.77 (2.62)	3.21 (2.01)	0.87; 0.75
15	8	7	9	16	152; 168	6.08 (3.32)	5.64 (4.33)	0.47; 0.5
16	8	21	5	26	142; 168	5.67 (3.37)	6.17 (4.11)	0.38; 0.75
18	7	37	36	73	95; 168	2.94 (2.46)	2.65 (1.73)	0.51; 0.64
19	10	11	0	11	157; 168	6.23 (3.03)	5.85 (3.67)	0.67; 0.78
21	7	13	14	27	141; 168	5.75 (2.86)	5.54 (2.82)	1.48; 1.44
24	11	18	3	21	147; 168	6.7 (3.65)	6.67 (4.21)	1; 0.45
26	8	17	10	27	141; 168	5.14 (3.98)	6.27 (3.5)	0.99; 0.42
29	7	20	0	20	148; 168	5.36 (3.77)	6.64 (4.08)	1.09; 0.47
Mean (SD)	9 (2)	20 (10)	9(10)	28 (17)	128; 21	5.16 (1.0)	4.98 (1.32)	0.82 (0.29); 0.65 (0.34)

Table A1. Trial exclusions for children.

Adult participant number	Age (y)	Erroneous saccades (n)	Saccade latency	Total number of exclusions	Total number of valid trials; total number of trials	Mean (SD) Number of trials per displacement level in no-blank condition	Number of trials per displacement level in blank condition	Normalized deviance no-blank; blank
17	21	2	0	2	166; 168	9.22 (4.47)	7.55 (4.55)	0.75; 0.51
20	24	6	11	17	151; 168	6.25 (4.37)	8.44 (4.3)	0.19; 0.29
22	25	15	4	19	149; 168	6.91 (5.11)	6.64 (4.82)	0.22; 0.31
23	23	2	0	2	166; 168	6.92 (4.62)	6.92 (4.08)	0.1; 1.32
25	25	8	12	20	148; 168	6.17 (4.28)	6.17 (4.15)	0.52; 0.34
27	25	21	1	22	146; 168	6.5 (4.6)	6.18 (4.47)	0.58; 0.23
28	19	40	4	44	124; 168	5.73 (3.72)	5.55 (3.62)	0.4; 0.18
30	21	7	1	8	160; 168	5.57 (4.38)	5.13 (3.59)	1.31; 0.7
31	22	8	0	8	160; 168	6.08 (3.8)	5.06 (3.45)	0.2; 0.8
32	23	9	4	13	155; 168	10 (5.13)	7.5 (4.43)	0.03; 0.05
33	20	19	1	20	148; 168	6.82 (4.42)	6.64 (4.01)	0.47; 0.16
34	22	1	0	1	167; 168	7.64 (4.15)	5.53 (4.61)	0.37; 0.92
36	24	14	6	20	148; 168	7.18 (4.33)	4.93 (3.97)	0.67; 0.32
38	22	3	1	4	164; 168	7.27 (4.41)	6.46 (4.59)	0.07; 0.45
40	23	0	0	0	168; 168	9.33 (6.56)	8.4 (5.36)	0.02; 0.41
Mean (SD)	23 (2)	10 (10)	3 (4)	13 (12)	155; 12	7.17 (1.35)	6.47 (1.14)	0.39 (0.35); 0.47 (0.29)

Table A2. Trial exclusions for adults.

Reference	Stimulus Type	Size (°)	Eccentricity (°)	Blank duration (ms)	JNDs (°) No-blank	Blank	Blanking effect Relative	Absolute (°)	Postsaccadic duration (ms)	Sample size (n)
Deubel et al. (1996)	Cross	0.2	6 or 8	250	1.00	0.50	0.67	0.50	Until response (∼500–1000 ms)	6
Ostendorf et al. (2010)	Cross	0.5	6 or 8	250	1.18	0.51	0.79	0.67	Until response (maximum 5 s)	8
Irwin & Robinson (2018)	Cross	0.8	6 or 8	300	2.07	0.87	0.82	1.20	Until response	12
Tas et al. (2012)	Dot	0.33	6 to 8	250	0.85	0.49	0.54	0.36	Until response	7
Tas et al. (2012)	Circular objects	0.65	6 to 8	250	0.97	0.72	0.30	0.25	Until response	7
This study (children)	Cartoon animal	2.39 × 1.76; 2.51 × 1.72	8 or 10	300	2.48	1.46	0.52	1.02	400	15
This study (adults)	Cartoon animal	2.39 × 1.76; 2.51 × 1.72	8 or 10	300	1.05	0.80	0.24	0.25	400	15

Table A3. Blanking effect and parameter comparison to previous studies.

Study	Initial saccade latency (ms)	Age (y)	Target amplitude (°)	Paradigm	Sample size per group (*n*)
This study, mean (SD)	186.4 (129) 162.1 (79.9)	7–12 19–25	8 or 10	Overlap paradigm	15
Cohen & Ross (1977)	∼273 ∼218	Mean 8.7 Unspecified adult	15 L/R	No warning signal	10
Cohen & Ross (1978)	∼258 ∼223	Mean 8.5 Mean 23.7	10 L/R	No warning signal	10
Munoz et al. (1998)	∼325 ∼250	9 23	20 L/R	Overlap paradigm	∼16
Salman et al. (2006), mean (SD)	248.7 (20.5) 253.6 (27.4)	8–19 —	10 R 10 L	—	39
Bucci & Seassau (2012)	∼300	9	15 L/R	Overlap paradigm	16

Table A4. Comparison of children and adult saccade latencies between this study and past studies. Where exact values were not provided in previous studies, we have approximated values from the published figures, at mean ages comparable to the ages tested in this study.